On Iridescent Plants

by

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Abstract

Plants with leaves of iridescent blue and green colour are common in the deep shade of Malaysian rain-forests. Simple anatomical observations have revealed that the green iridescence is due to the refraction of diffuse light onto specially-oriented chloroplasts by lense-shaped cells. Blue iridescence colour is due to the operation of thin film interference filters in or on the epidermis. The advantage of such a filter in forest shade plants is the effective absorption of red wavelengths of light at the expense of the reflection of less important blue wavelengths. This report documents iridescence in the leaves of many unstudied taxa (mainly pteridophytes), common in Malaysian rain-forests.

Life in a tropical rain-forest is not quite as easy for green plants as popular accounts would indicate. First by, the forest soils are generally rather sterile. Secondly, plants are under intense pressure of predation by insects and other animals. Finally, the light conditions are frequently less than optimum—from very bright conditions in the canopy to deep shade on the rain-forest floor. In this discussion we are concerned with the deficiency of light in the shade at the bottom of the rain-forest; in this environment can be seen a number of plants whose leaves display brilliant blue and green colours. These colours can be described as *iridescent* because of their intensity and metallic quality. The association of these iridescent plants with the shady and moist environments has compelled many naturalists to reason that the colours must be associated with adaptations which help the plants to survive in the dark habitats. The rain-forest floor is one of the darkest environments in which plants grow. Not only is the total light quantity a small fraction of that above (less than one percent) but also the light quality is diminished; more of the wavelengths vital to photosynthesis, with the exception of some red light, have been absorbed by the foliage overhead (Evans, 1966; Federer and Tanner, 1966; Bjorkman, 1972). The purpose of this discussion is to explore how the iridescence of some Malaysian plants is associated with adaptations to increase the absorbance of diffuse and weak light for maximum photosynthetic efficiency.

LEAF ANATOMY AND FUNCTION

Leaves possess many structures which are significant in the efficient absorption of light in shady environments (see Ray, 1972; and Esau, 1965). Figure 1 summarizes these structures.

The Cuticle. The function of the cuticle is two-fold (see Martin and Juniper 1970 for further details). First, it repels water and prevents the rapid dessication of the leaf. Secondly, it can act as a selective filter in reflecting harmful ultraviolet light, and allowing the absorption of visible light essential for photosynthesis.

The Epidermis. This superficial cell layer, particularly on the upper leaf surface, may possess special adaptations for efficient light absorption. It may have bumps which remain dry when the lower areas are covered by rainwater; these allow more efficient light absorption in wet conditions (Haberlandt, 1914).

Epidermal cells may also have regularly convexly curving upper surfaces; these focus diffuse sunlight onto specially orientated chloroplasts. Finally, the epidermal cells of extremely shade-tolerant plants (especially pteridophytes) may contain chloroplasts which can more directly receive light before it is scattered by the cell walls.

Photosynthetic Parenchyma. Both the palisade and spongy mesophyll layers may have special adaptations for low light environments. They may be specially oriented beneath the lens-like epidermal cells. In shade-tolerant plants these cells would have fewer and larger chloroplasts. The protein/chlorophyll ratio, which reflects the relative plant investment in light reception versus biosynthetic apparatus, would be low. Finally, the cells may be closely packed together to minimize the reflection (and loss) of light between the cells.

Stomata. In low light environments the stomata will not be a limiting factor, and we might expect various arrangements on the upper and, especially, lower leaf surfaces.

Leaf Size and Shape. In low light environments leaves tend to be large and thin, with a high surface/volume ratio. This ratio is increased even more in plants, as ferns, with highly divided leaves.

Thus, the task in understanding the significance of iridescence in shade-tolerant plants is to explain how some attributes of leaf structure confer an advantage on the plants and, at the same time, physically account for the iridescent colour.

IRIDESCENCE

Many plants from diverse taxonomic groups, from humid rain-forests throughout the tropics, possess iridescent leaves (Richards, 1952). Iridescent plants can be observed in Malaysian rain-forests (see Table 1), and some are extremely common. *Selaginella willdenowii* is a scandent pteridophyte frequently encountered in rain-forests, plantations and belukar throughout Southeast Asia. Another pteridophyte, *Athyrium crenatoserratum,* can be frequently observed in local rain-forest, as is *Phyllagathis rotundifolia* (Melastomataceae). Blue-leaved sedges of the genus *Mapania* commonly grow in Sarawak rain-forests. Others are less common. The two kinds of iridescence observed in these plants, green and blue, are discussed separately below.

Green Iridescence. The first observations on green iridescence were made on the cave moss, *Schistostega,* which grows in caves and other dark and wet environments in Europe and North America. Richards (1932) reported that the brilliant green colour encountered at particular angles was due to the functioning of certain protonemal cells as refractive lenses, focussing the diffuse light onto the specially oriented chloroplasts. Analysis of Malaysian green iridescent plants indicates that the same principles operate (see Figure 2 and Plate 1). These plants all share cells (epidermal or palisade) whose outer walls have a uniform convex curve. The chloroplasts are always oriented at the distal end of these cells. When we look at these plants the intense green colour can be observed only at an angle perpendicular to the surface of the plant. At other angles the colour is dull green or even whitish. This effect is due to the focusing of the diffuse light into a more intense beam directly onto the chloroplasts. These organelles, with their parallel stromal organization, absorb the light useful in photosynthesis and reflect the unused green light directly out of the long cells. Thus when we look at these plants, as at the entrance to Batu Caves near Kuala Lumpur or on rocks in especially shady forest habitats, we see the green light reflected in an intense and narrow beam. At other angles the light appearance of the leaves is due to reflection of whole light off of the cell surface acute angles and also the scattering of light within the cells. The birefringence of the cellulosic walls may also be a factor affecting the quality of the light reflected at acute angles.

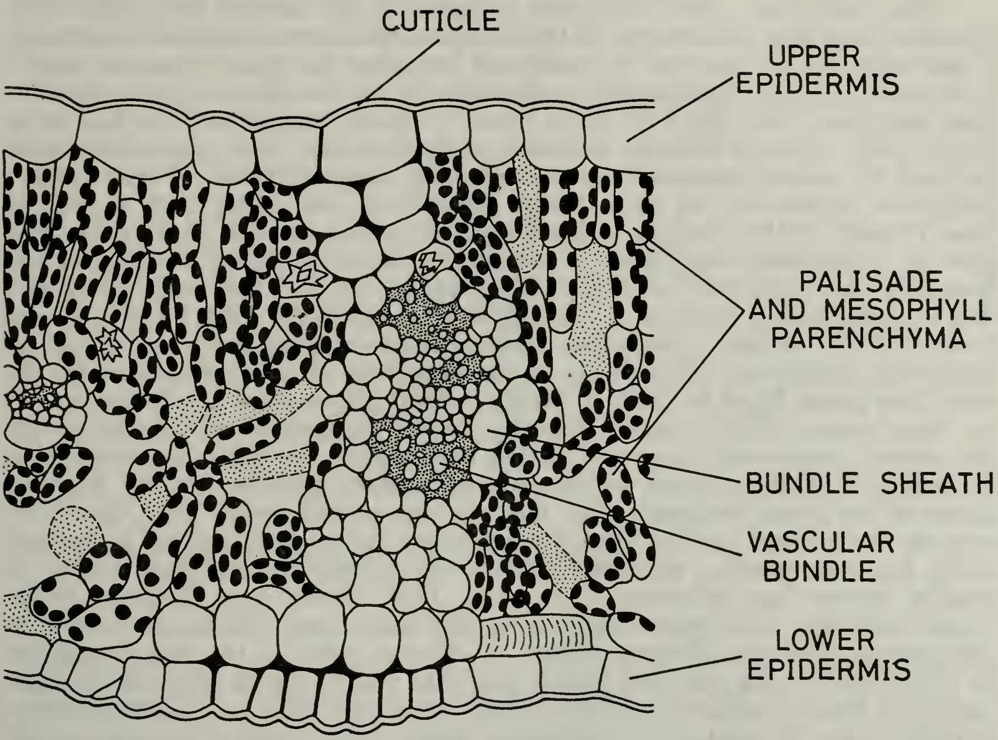
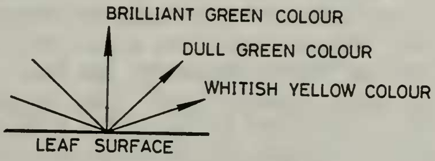


Fig. 1. A diagram of the typical structure of a leaf.



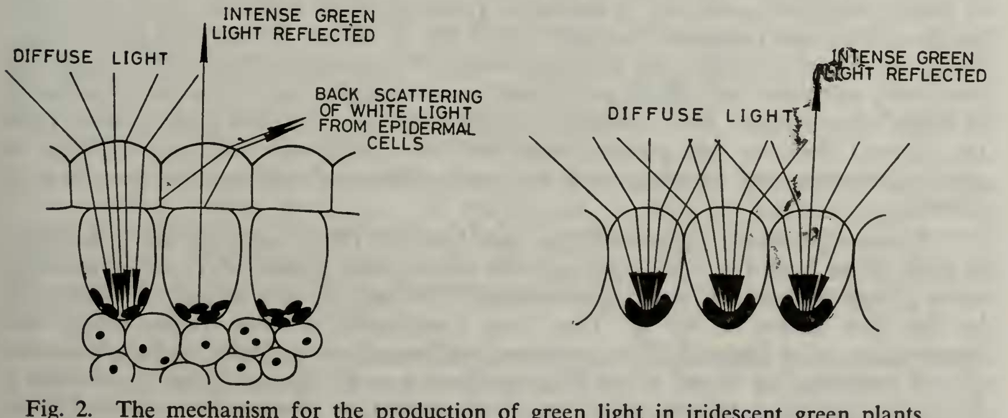

INTENSE GREEN LIGHT REFLECTED
DIFFUSE LIGHT
BACK SCATTERING OF WHITE LIGHT FROM EPIDERMAL CELLS
INTENSE GREEN LIGHT REFLECTED
DIFFUSE LIGHT

Fig. 2. The mechanism for the production of green light in iridescent green plants.

Blue Iridescence. Men have been intrigued by the startling blue plants ever since they were first encountered. In the Malaysian rain-forest *Selaginella willdenowii* is the most striking example. In traditional languages the name "peacock plant" is frequently used to describe these pteridophytes (as the Malay "paku merak"). One aboriginal Senoi name for these plants translates roughly as "the hair on a tiger's rump" (Gerard Diffloth, personal communication). These plants have been included in various medicinal remedies probably simply because of their colour. *Selaginella willdenowii* has been used in preparations for aching back as well as fever (Burkill, 1935). European scientists made frequent mention of the colour but gave no explanation. Stahl (1896) studied *S. willdenowii* while working in the famous Treub Laboratory at Bogor. He observed that the iridescent colour was due to pigmentation granules in the cuticle. Fox and Wells (1971) and Lee and Lowry (1975) recently published more adequate explanations for colour in *Selaginella willdenowii*, likely also to be the mechanism of colour formation for the other blue plants listed in Table 1. Stahl's original observations can be discounted for three reasons. There are no presently known pigments in pteridophytes with the spectral properties to account for the blue colour. Secondly, in re-examining the epidermis of these plants we observed no pigment granules. Thirdly, the blue colour of the leaves disappears when they are covered with water. Thus, the colour must be due to some physical optical effect of the leaf surface, and not a pigment. There are three physical phenomena which can account for iridescent colour as seen in insects (see Michelson, 1911; Fox, 1959; Neville and Caveney, 1969). These could also be invoked to explain the blue leaf colour. Diffraction of light on thin gratings disperses different colours at different angles to the object's surface. In *S. willdenowii* and the other plants, only blue colour can be observed. Tyndall scattering (which explains blue sky colour) polarizes light; no polarizing effects have yet been observed in any iridescent plants. Light interference, due to thin films, can produce uniform colours over relatively wide angles of incidence, and is the likely physical explanation of the phenomenon.

The principle of a thin film (or quarter wavelength) interference filter is not familiar to most biologists, and requires some explanation. As a specific example, if the conditions described in Figure 3 are met, optical interference will result in the differential absorbance and reflection of different wavelengths of light. First, the filter must have a slightly different refractive index (r) than the surrounding medium, the air above or the cell below. Secondly, the filter must be exceedingly thin, a fraction of the wavelength of visible light. Thus, in the filter described in Figure 3, the thickness (142μ) is fraction of red visible light at 600 μ. If we trace the path of blue light (at 405 μ) through this filter, we see that light of this wavelength will be reflected by the filter. The distance travelled from A and back to C equals the wavelength of that light in the filter. Retarding the light by one wavelength puts the light (visualized as a transverse wave) in phase, and the energy at this wavelength moves out of the filter. However, light with four times the wavelength of the filter thickness (or red light of 795 μ) would be retarded half a wavelength at the same point, and its energy would be nullified. Thus such a filter can selectively enhance the reflection of certain wavelengths and allow the absorbance of other wavelengths. Two common examples are the rainbow colours seen from the thin oil films on rain puddles, and also the special anti-reflection coatings on quality cameras and binoculars. For a more technical explanation see Vasicek (1960).

To test the above hypothesis Lee and Lowry (1975) analyzed the reflectance of light from both the iridescent and the older green leaves of *S. willdenowii* by using a slightly modified spectrophotometer. The analysis gave a peak of reflectance by the blue leaves at 405 μ. They then constructed a filter model fitting this observation, as in Fgure 3. They assumed a filter refractive index slightly in excess of cell contents (of about $r = 1.35$), or about $r = 1.4$ as in Figure 3. In such a filter a concellation of the reflection effects would be observed at about 530 μ,

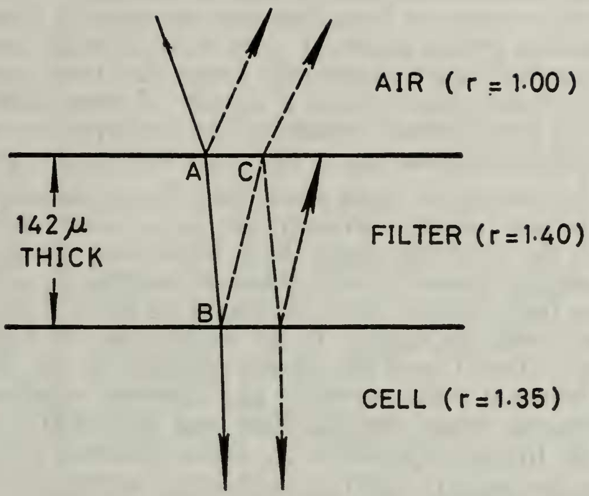


Fig. 3. Operation of a simple thin film interference filter.

1. REFLECTS BLUE LIGHT.

IN THE FILTER, AT AN EFFECTIVE WAVELENGTH OF 284 μ, THE LIGHT IS DELAYED ½ WAVELENGTH AT POINT *B* AND IS NULLIFIED — CANCELLED AS OVERLAPPING TRANSVERSE WAVES WOULD SHOW. AT POINT *C* LIGHT IS DELAYED A FULL WAVELENGTH AND IS REFLECTED OUT — WAVES COINCIDE. AT THIS POINT THE REFLECTED LIGHT HAS A WAVELENGTH OF 405 μ (1.4/1.0 x 284) AND IS BLUE.

2. NO EFFECT ON LIGHT AT 530 μ

AT 2⅔ THE FILTER THICKNESS THE WAVES WOULD CANCEL.

3. ABSORBS RED LIGHT.

IN THE FILTER LIGHT AT A WAVELENGTH of 568μ IS DELAYED ½ WAVELENGTH AT *C* AND IS NULLIFIED — CANCELLED AS OVERLAPPING TRANSVERSE WAVES WOULD SHOW. THUS MORE OF THIS LIGHT PASSES THROUGH THE FILTER AT *B*. HERE THE EFFECTIVE WAVELENGTH IN AIR IS 795 μ (568 x 1.4/1.0) AND IS RED.

with increased absorbance at higher wavelengths. In the difference spectrum obtained by subtracting values of the green leaves from the blue leaves; a curve similar to that predicted was observed (see Figure 4). Light above 700 μ would be reflected by all leaves (Gaussman and Allan, 1973; Gates *et al.*, 1965) and would obscure the filter effect at greater wavelengths. Thus, we have good physical evidence that such filters operate in the blue plants.

The operation of such a filter has obvious adaptive significance for these shade-tolerant plants. Blue light (of which there is little in the dim light of the forest floor) is reflected, and the red light, which is more significant in the total photosynthesis by these plants, is absorbed. Thus, these filters can operate as "anti-reflection" coatings which increase the absorption of photosynthetically active light on the shady forest floor.

Selaginella willdenowii plants possess additional adaptations to increase photosynthetic efficiency. Firstly, the epidermal cells contain single large chloroplasts at the distal ends of the cells (see Plate 2). Thus, most of the photosynthesis occurs just below the leaf surface. Secondly, the epidermal cells have regularly convexly curved surfaces which appear to focus light onto the specially oriented chloroplasts, as previously described for the iridescent green plants. Finally, the iridescent leaves have protein/chlorophyll ratios significantly lower than those exposed to the sun (Krishnan, 1975). These plants possess a number of remarkable adaptations for the improvement of photosynthetic efficiency. The analogy of a camera with coated lenses and high speed film seems apt in describing the function of these plants.

The other blue plants (see Table 1 and Plate 2) are different from *Selaginella willdenowii* in several details, although the same colour-producing principle probably operates for all of the plants. In *S. willdenowii* the blue colour can be removed by dipping the plants in water (blueness reappearing after drying). Other plants do not lose their blueness upon immersion. In the first case, the filter must be in some contact with the surface. In the second case the filter is likely to be found within the cell wall, and not directly exposed to the air. Scans of leaf reflectance for *Athyrium crenatoserratum* and *Lindsaea scandens* are similar to *Selaginella willdenowii*, except that the blue peak is at 410 μ in *Lindsaea* and 415 μ in *Athyrium*. In both of the flowering species observed, *Phyllagathis rotundifolia* and *Begonia pavonina*, I could not ascertain the wavelength of the blue colour because the colour was effectively produced when the incoming light was at a smaller angle to the surface than the reflected light. The method of measurement required a fixed incident angle of 60° for both. The physical constitution of the filters is not presently known, but in all cases the colour is due to a physical optical effect and not to a pigment.

Other blue plants possess distinct anatomical features in addition to *Selaginella willdenowii*. In *Athyrium crenatoserratum* (Plate 2), the epidermal cells also contain chloroplasts, and the outer wall has the convex curve described above. The blue colour is particularly apparent in the older leaves of this common fern. Perhaps the most spectacular iridescent blue plant of all is the rare begonia, *Begonia pavonina*. When looking directly at these plants one sees an intense dark blue colour. However, if the angle of observation is changed so that light is reflected at a more acute angle, the colour changes from blue to dull green and then to gold. An interference filter would account for the blue colour, and the gold colour is probably due to the refractive properties of the epidermal cells. The plant is now under further study. The chloroplasts of *Begonia pavonina* are at the bottom of the palisade parenchyma cells. Both light refraction and interference appear to enhance light absorption in this plant, as in *Selaginella*. The palisade cells are packed very closely together to minimize light loss due to scattering effects. Immediately beneath is a compact mesophyll layer, the cytoplasms of which is dark red with anthocyanins. This layer probably reflects red light (comparatively more abundant on the rain-forest floor) right back up to the chloroplasts in the palisade cells. Thus the *Begonia pavonina* plants appear to have leaves with lenses, filters and special mirrors—all to increase conversion of precious light energy to sugars in the shady forest environment.

FURTHER RESEARCH

Rain-forest floor plants, as in Malaysia, have some spectacular adaptations for the efficient utilization of light. Further studies may uncover new principles, and will help illuminate the functional significance of anatomical details of leaf structure. I see some specific areas of research potential.

First, although there is now some evidence for the operation of thin film interference filters in plants, no one has yet been able to elucidate the structural basis of the filter in the different plants. Lee and Lowry (1975) discounted the

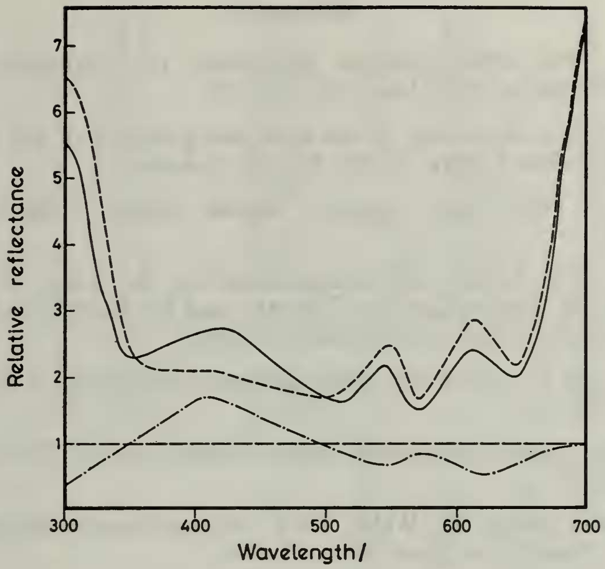


Fig. 4. The relative reflectance of light by green (— — — — — — —) and blue (——————) *Selaginella* leaves as recorded by a spectrophotometer. The bottom curve (—·—·—·—·—) is the difference between the two curves above and gives a plot similar to that expected for a thin film interference filter.

cuticle as being the molecular basis of the filter in *S. willdenowii;* non-polar solvents, which dissolve cuticle waxes, did not remove the interference. Fox and Wells (1971) speculated that the structural basis for the optical effect may be the trapping of thin layers of air by the epidermis, as is well known for some insects. Critical experimental support for the optical phenomenon of interference should include physical information on the nature—including the thickness and refractive index—of the filter. The small dimensions will necessitate the use of sophisticated electron microscope techniques. If the thickness and refractive index of the filters were known, then we could precisely predict the nature of the interference effect. The basis for the filter may well lie in the orientation of cellulose microfibrils in the cell wall; further research will solve this problem.

Rather esoteric studies on the leaves of shade-tolerant plants may eventually be of some practical importance. In designing more efficient plantation agriculture systems for the tropics, biologists will have to consider the kinds of plants to grow in the understoreys of the plantations. Knowledge of leaf structure may help us select plants which could thrive in such environments. Who knows? maybe someday we will spray interference filters onto the leaf surface of understorey plants, making them blue—and more productive.

Acknowledgements

The following individuals were extremely helpful in the various stages of the preparation of this manuscript. Prof. R. E. Holttum gave encouragement and additions to Table 1; Mr. Willis Littke also gave additions. Drs. B. C. Stone, J. B. Lowry and Peter Ashton, and Prof. Paul Richards gave advice and encouragement. Prof. Anne Johnson identified the liverwort. Encik Jayamohan Krishnan and Encik Ho Kok Wai provided photographs; Cik Tan Geok San gave technical help and Cik Wan Shahrizah typed the manuscript.

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Table 1. A list of iridescent plants observed in Malaysia

TAXON	FAMILY	DISTRIBUTION	COMMENTS
GREEN PLANTS			
Cyathodium foetidissimum Schffn.	Marchantiaceae (Hepacopsida)	S. E. Asia	Seen at mouth of dark cave, Batu Caves, this and other taxa that grow in very dark locations appear iridescent green.
Monophyllaea patens Ridl.	Balsaminaceae	Limited to a few limestone outcrops in W. Malaysia.	Seen inside sanctuary cave Batu Caves. The related *M. horsfieldii* Ridl. is iridescent, but to a lesser extent.
Begonia sinuata Wall.	Begoniaceae	S. E. Asia	Common on shady and damp rocks in forest. Other *Begonia* species also have iridescent green leaves, but to a lesser extent.
BLUE PLANTS			
Selaginella willdenowii (Desv.) Bak.	Selaginellaceae	Extremely common in S. E. Asia and also in temperate greenhouses.	Perhaps the most frequently encountered blue-leaved plant. Other species may also be iridescent, AS *S. atroviridis* (Wall.) Spring.
Lindsaea scandens Hk. var. *terrestris* Holtt.	Dennstaedtiaceae (Lindsaeoideae)	Low forest and mountain valleys throughout the peninsula.	Other species of *Lindsaea* (perhaps L. *ucida* Bl.) may have a blue metallic sheen to the leaves.
Athyrium crenatoserratum (Bl.) Milde	Dennstaedtiaceae (Athyrioideae)	Common in low and mid-elevation forest in S. E. Asia.	The older leaves have a metallic blue sheen. Also reported for *Athyrium cordifolium* (Bl.) Copel.
Polystichopsis hanifii (Holtt.) Holtt.	(Dryopteridoideae) Dennstaedtiaceae	In high mountain valleys, West Malaysia.	
Phyllagathis rotundifolia Bl.	Melastomataceae	Common in low elevation forest in South East Asia.	After *S. willdenowii* the most common blue iridescent plant.
Begonia pavonina Ridl.	Begoniaceae	Rare in West Malaysia. Deep forest from low to high elevation.	Striking for the bluish-purplish coloured leaves, this turning to gold as the leaf is turned.
Mapania sp.	Cyperaceae	South East Asia.	Common iridescent blue plants in Sarawak.
Didymochlaena Truncatula (Sw.) J. Sm.	Dennstaedtiaceae (Dryopteridoideae)	West Malaysia, and perhaps elsewhere in South east Asia.	at medium elevations in mountain areas.